On Reflex Inhibition of the Knee Flexor.

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1. Introduction.

Study of reflex inhibition has been prosecuted more with extensor centres than with flexor. In the case of these latter, the experimental examination of the inhibition is of necessity somewhat differently circumstanced than in the case of the extensors. For both there is requisite a suitable background of reflex excitement against which inhibition may be evident. With the extensors this reflex background of excitement can be provided by postural tonus, and such tonus is readily obtained by use of the decerebrate preparation. With the flexors there is at present no procedure available for providing such tonic preparations. Recourse has to be taken to the production of reflex excitation of the centres by artificial stimuli applied to some appropriate afferent channel.* The background of contraction of the flexor muscle against which inhibition can become apparent is thus obtained by more artificial means. This latter procedure has its drawbacks; the background of reflex excitement it provides is less mild and less enduring than that furnished by natural tonus, and it is less enduring exactly in those approximately milder degrees which are particularly favourable for the manifestation of inhibition. On the other hand there are compensations, one being the more complete and rapid variation of the background in regard to its medium and higher intensities.

2. Method Employed.

As muscles typical of the flexor class we have chosen for our observations *semitendinosus* and *sartorius* (cat). These have been shown† to engage regularly as flexors, of knee and hip respectively, in the nociceptive flexion reflex of the limb, in the reflex step in its flexion phase, and in the scratch-reflex. Each of these muscles is readily prepared for the myograph by detachment of the lower tendinous insertion and liberation of the whole distal half of the muscle, the nerve and blood supply which enter above remaining intact. To immobilise the preparation the procedure has been as follows:—(1) Nerves severed: peroneal, popliteal, small sciatic, femoralis, obturator, external cutaneous and hamstring nerves of both limbs, with the exception in the case of the semitendinosus preparation of the branch to that muscle from the hamstring nerve of one limb, and in the case of the

* Sherrington, 'Roy. Soc. Proc.,' 1909, B, vol. 81, p. 251.

† Sherrington, 'Journ. Physiol.,' 1910, vol. 40, p. 28.

sartorius preparation of the branch to that muscle from the femoralis nerve of one limb. (2) Muscles resected: glutei tensor fasciæ femoris, psoas and psoas parvus, and all muscles attached to the femoral trochanters and intertrochanteric line. (3) The animal lying supine, with hips and knee semi-flexed, steel drills are inserted into the innominate bone, the outer femoral condyle and the lower end of tibia in both limbs; these drills are then clamped to heavy immovable uprights on the experiment table. These steps, as well as the whole of the preceding decerebration, are carried out under deep chloroform narcosis. For registration of the results a thread from the freed muscle tendon is carried over a light running pulley to a horizontal myograph. The tension of a light spiral spring is arranged to stretch the muscle to about its ordinary resting length. For stimulation of the afferent nerve or nerves we have employed faradism, or series of brief constant currents of alternating direction given by a v. Kries rotating rheonome* fed by four Leclanché cells, a graduated 100 ohms resistance box being in the main circuit. The electrodes have been non-polarisable, either of the du Bois-Reymond clay pattern or of the Utrecht pattern devised by Noyons.

The general plan adopted for the examination of the reflex effect of any particular afferent upon the flexor centre consisted in throwing that centre into reflex excitement as documented by contraction of the flexor muscle attached to the myograph, and then, while that contraction was in progress, stimulating the afferent nerve whose special influence on the centre it was desired to observe. This latter stimulation may be termed the intercurrent stimulation; the stimulation which provides the background contraction, against which the effect of the intercurrent stimulation has to show, may be termed the background stimulation.

3. Results.

i. *Influence on the Knee Flexor (semitendinosus) exerted by Afferent Nerves of the Contralateral Hind-limb.*

The afferent nerves tested have been contralateral peroneal and popliteal, either separately or both together. The background excitation has been provided by stimulation of the corresponding nerves of the ipsilateral limb.

The effect of the contralateral afferent as thus tested is preponderantly inhibition. This preponderance of inhibition is very great. It holds for a wide range of intensities of stimulation. Its degree may be sufficient to entirely efface all trace of the background contraction. The inhibition is stronger the stronger the intercurrent stimulus (fig. 1, *a*, *b*, *c*), but it results in many cases from even quite weak intensities of stimulus.

With weak intensities of contralateral stimulus the effect is, however, not always inhibition. Such stimulation quite frequently causes contraction, *i.e.* augments the intensity of the contraction (fig. 2, *a*, *c*; fig. 3, *b*). The amount of contraction which it provokes is never in our experience large,

* R. Metzner, 'Archiv f. Physiologie,' 1893, Supplement-Band, p. 84.

although quite distinct and unmistakable. The contraction which weak stimulation of the contralateral afferent thus produces tends, while the stimulation is in progress, to subside and be replaced by inhibitory relaxation.

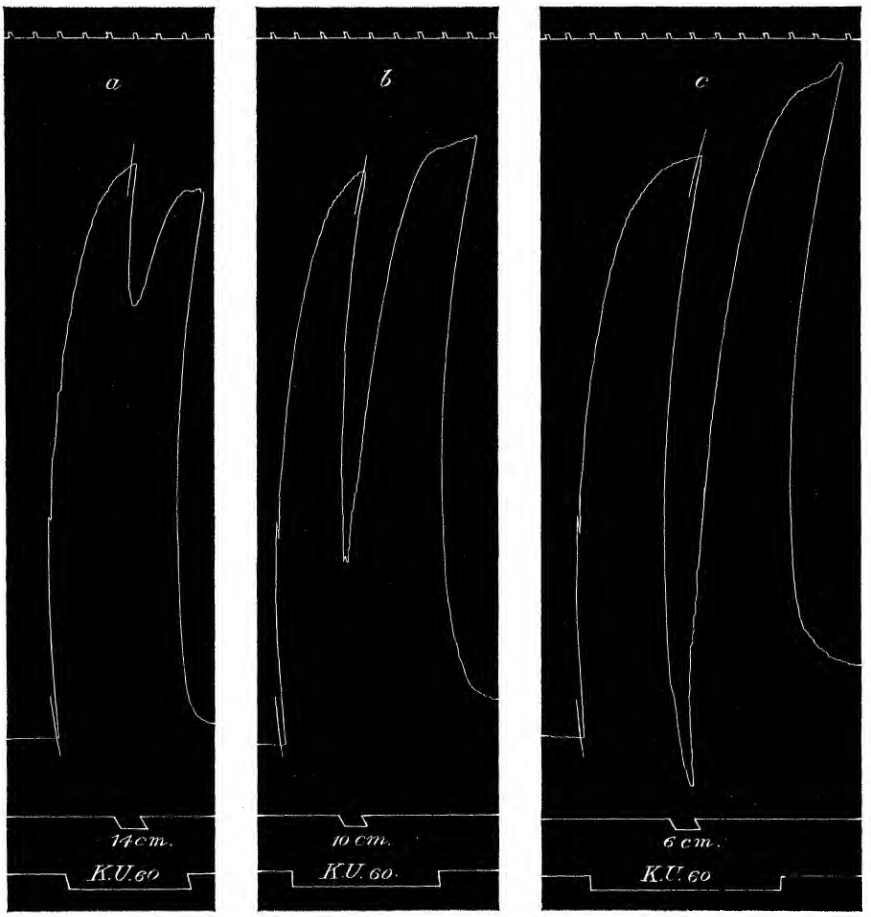

FIG. 1.—Inhibitions of the knee flexor, *semitendinosus* (cat, decerebrate). Lower signal marks stimulation (faradic) of ipsilateral afferent (peroneal + popliteal) exciting reflex contraction of the muscle. This stimulus remains of the same intensity, namely, 60 units of the scale of the Kronecker inductorium, in all three of the successive observations *a*, *b*, and *c*. Upper signal marks stimulation (faradic) of the contralateral afferent (peroneal + popliteal); this intercurrent stimulus is stronger in *b* than in *a*, and in *c* than in *b*, the secondary coil being at 14 cm. in *a*, at 10 in *b*, and at 6 in *c*. Time, in seconds, above.

The result given by the intercurrent stimulus then is an initial contraction followed by an ensuent inhibition (fig. 3, *d*). As the strength of the stimulus is increased, the initial contraction becomes more brief and less ample, and the ensuent inhibition appears earlier and is more pronounced. By further

increase of the stimulus, inhibition without any apparent contraction at all results. As the strength of stimulus is increased further still, the only

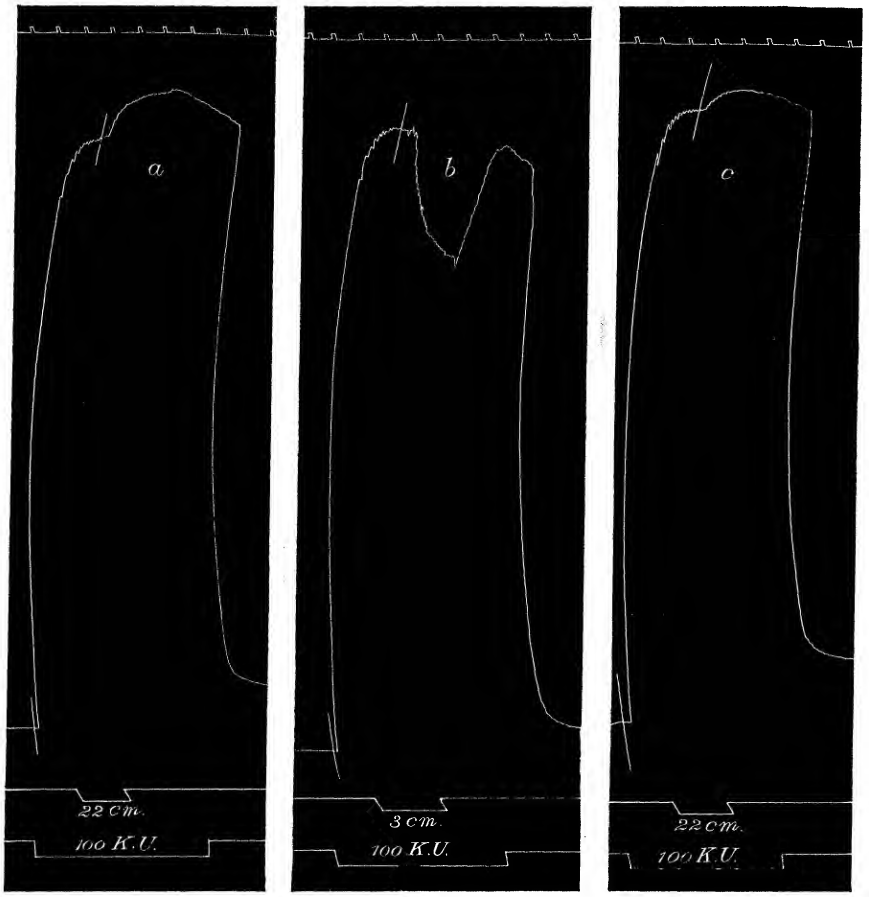

FIG. 2.—Reversal of reflex effect on increasing the intensity of the intercurrent stimulus, its result changing from contraction to inhibition. *Semitendinosus* (cat, decerebrate). Lower signal marks stimulation (faradic) of ipsilateral afferent (peroneal + popliteal) giving reflex contraction of the muscle. This stimulus remains of the same intensity, namely, 100 units, Kronecker inductorium, in all three of the successive observations. Upper signal marks stimulation (faradic) of the contralateral afferent (peroneal + popliteal); this intercurrent stimulus is quite weak (secondary coil at 22 cm.) in *a* and *c*, but in *b* is strong (secondary coil at 3 cm.). Time, in seconds, above.

further change in the reflex effect is that the pure inhibition becomes more prompt and more profound.

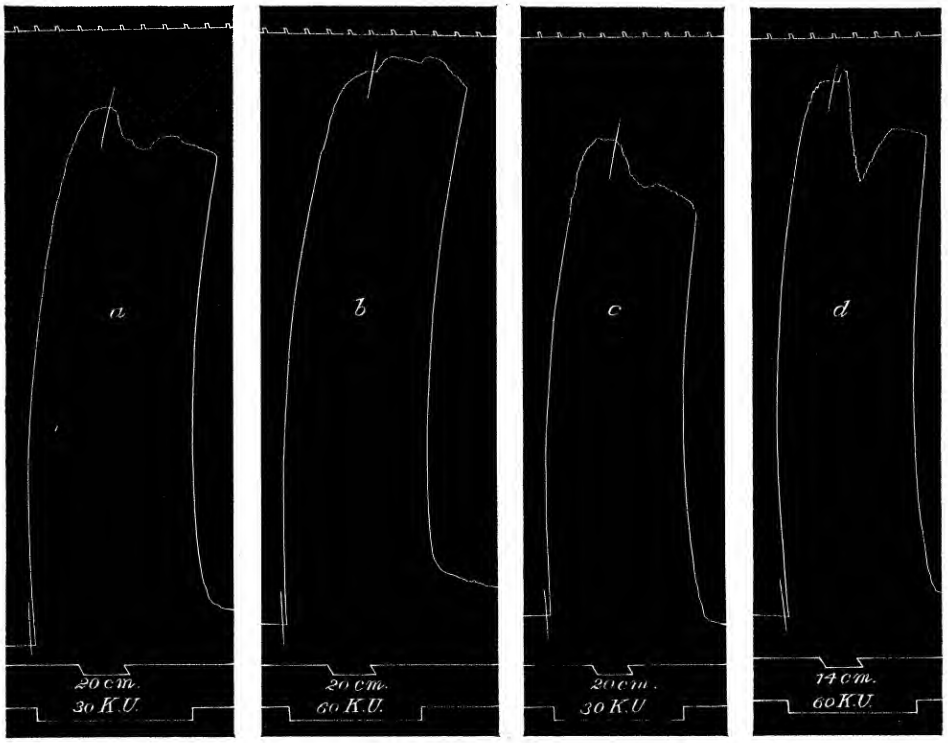

FIG. 3.—Influence of intensity of background-reflex on effect of intercurrent reflex. *Semitendinosus* (cat, decerebrate). Lower signal marks stimulation (faradic) of ipsilateral afferent (peroneal + popliteal). This stimulus in *b* and *d* is 60 Kronecker units; in *a* and *c* it is weaker, namely, 30 Kronecker units. Upper signal marks stimulation (faradic) of contralateral afferent, and is of the same intensity, namely, secondary coil at 20 cm. for observations *a*, *b* and *c*, but for *d* it is stronger, namely, coil at 14 cm. In *a* and *c* the effect of the intercurrent stimulus is inhibitory, in *b* it is pressor, *i.e.* augmentative of contraction; in *d* it is pressor also, but the increased contraction is followed by inhibition. Time above, in seconds.

ii. *Influence of the Background Contraction on the Effect obtainable from the Intercurrent Contralateral Stimulus.*

It was shown in a previous communication that when two afferent nerves with mutually opposed influence on the same muscle are stimulated concurrently the effect on the muscle is an algebraic summation of the contraction and inhibition belonging to the two nerves respectively. Some of the examples then cited were furnished by the same muscle, semitendinosus, and the same afferents as chiefly employed in the present observations, and the present observations have confirmed the foregoing. They have also extended them in the following respect: Suppose a weak contralateral stimulus is chosen, such that it produces slight inhibition of a

background contraction which is itself of rather weak intensity. If then the intensity of the background contraction be increased by stimulating the ipsilateral afferent more strongly, the inhibitory decrement produced by the contralateral stimulus becomes less, *i.e.* produces a shallower notch in the contraction myogram, in accordance with the above rule. If, however, the intensity of the background contraction be increased still further beyond a certain limit, which need not be very extreme, the effect of the intercurrent stimulation of the contralateral nerve is changed from inhibition to excita-

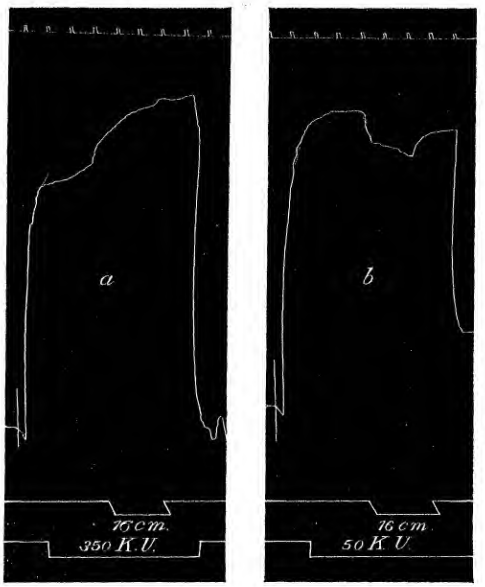

FIG. 4.—Decrease of background intensity changes the effect of a given intercurrent reflex from a pressor influence to a depressor. *Semitendinosus* (cat, decerebrate). Lower signal marks stimulation (faradic) of ipsilateral afferent (peroneal); the stimulus is more intense in *a* (350 Kronecker units) than in *b* (50 Kronecker units). Upper signal marks stimulation (faradic) of contralateral afferent (popliteal) and is of the same intensity in *a* and *b*. In *a* it augments the contraction, in *b* it decreases (inhibits) it. Time marked above, in seconds.

tion, *i.e.* the contralateral afferent not only does not obviously diminish the contraction but augments it (fig. 3, *a* and *b*; fig. 4, *a* and *b*).

Besides intensity, other conditions also attaching to the background stimulation influence the effect of the contralateral nerve. In our experience the background of reflex contraction obtained by use of the brief alternating galvanic currents of the v. Kries rheonome for the ipsilateral afferent is more readily and amply inhibited by the contralateral afferent than is the reflex contraction furnished by ordinary faradism (fig. 5, *a*, *b*, *c*, *d*). Similarly, the

inhibitory influence of the contralateral afferent is particularly easily and strikingly obtainable when pitted against the after-discharge contraction which frequently follows and prolongs, for a short time, a strong reflex after the strong stimulus which excited the contraction has been itself withdrawn. So also the inhibitory effect is markedly well obtained against the contraction elicited by a mechanical stimulus applied to the pinna of the ear. Occasionally in the decerebrate preparation the semitendinosus enters into somewhat prolonged reflex contractions whose source is not clear (fig. 6); and against

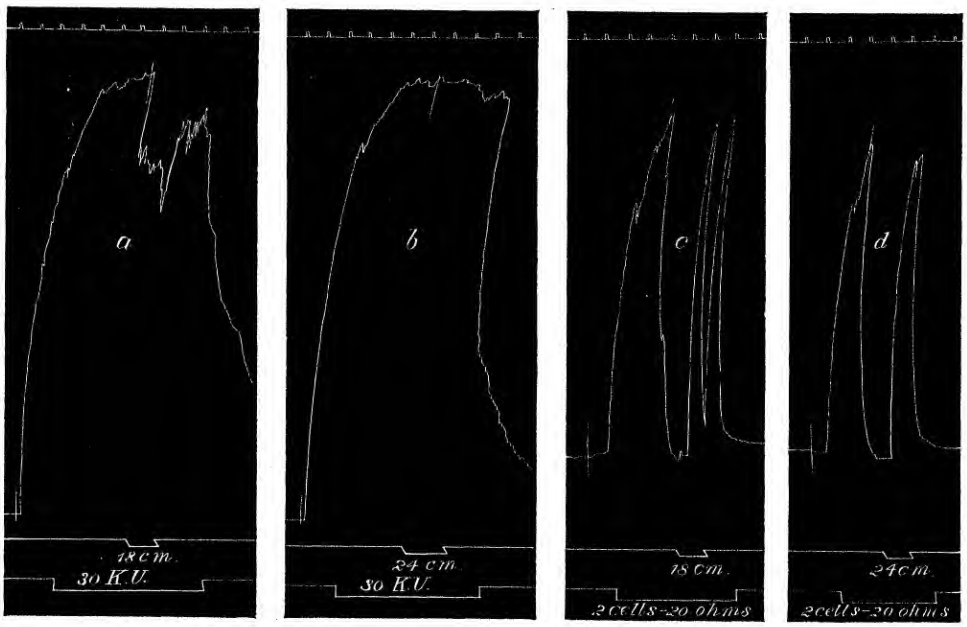

FIG. 5.—Similar intercurrent stimuli opposed to reflex backgrounds given by faradic and galvanic stimuli respectively. Lower signal marks stimulation of ipsilateral afferent by weak faradisation (30 Kronecker units) in *a* and *b*, by galvanic currents delivered by v. Kries rheonome in *c* and *d*. Upper signal marks weak stimulation (faradic) of contralateral afferent, secondary coil at 18 cm. for *a* and *c*, at 24 cm. for *b* and *d*. The inhibitory effect is more marked against the galvanic background. Time above, in seconds. *Semitendinosus* (cat, decerebrate).

these also the inhibitory effect of the contralateral afferent is extremely easily exerted.

And there is a further factor attaching to the background stimulation which likewise influences the effect of the contralateral afferent. When a given contralateral stimulus is repeated at intervals during the course of a prolonged reflex contraction, its inhibitory effect is greater in the later repetitions than in the earlier. This increase is regularly progressive and is often very marked (fig. 7, also fig. 6). It shows itself particularly when the reflex

contraction is on the wane as judged by decline in the height of the myogram. It shows itself also when the intercurrent contralateral stimulus is repeated at a time when the reflex, as judged by the myogram curve, is exhibiting no marked decline, but remains as high, or almost as high, as it was at outset. It would seem, therefore, that, as the excitatory reflex proceeds, some central

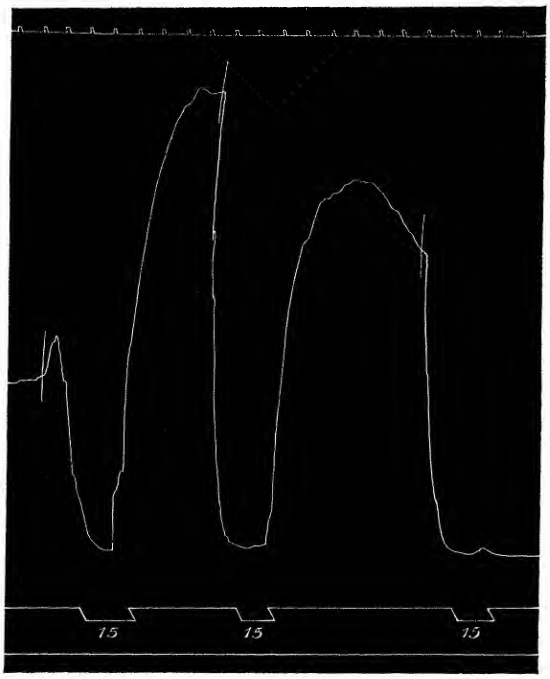

FIG. 6.—*Semitendinosus* (cat, decerebrate). At outset of the observation the muscle was already in contraction owing to some reflex the origination of which was not clear. The contralateral afferent (peroneal with popliteal) was then (left-hand notch of signal) faradised; this caused a transient increase of contraction, followed during the stimulation by marked inhibition, and succeeded, on withdrawal of the stimulus, by a rebound contraction. On repetition of this stimulus (middle notch on signal line), a marked inhibition again occurred, but without initial increase of contraction and followed after withdrawal of the stimulus by less marked rebound. On a third repetition (right-hand notch of signal line) the stimulus caused inhibition even more prompt than before, and no rebound contraction followed its withdrawal. Time marked above in seconds.

change ensues very soon after the reflex has reached its maximum, which renders the reflex discharge more and more open to inhibitory decrement. In other words, *fatigue* of the background reflex seems to favour markedly the operation of inhibition against the reflex.

Further, when the contralateral afferent under a given stimulus of weak intensity produces the reflex augmentation of the background contraction

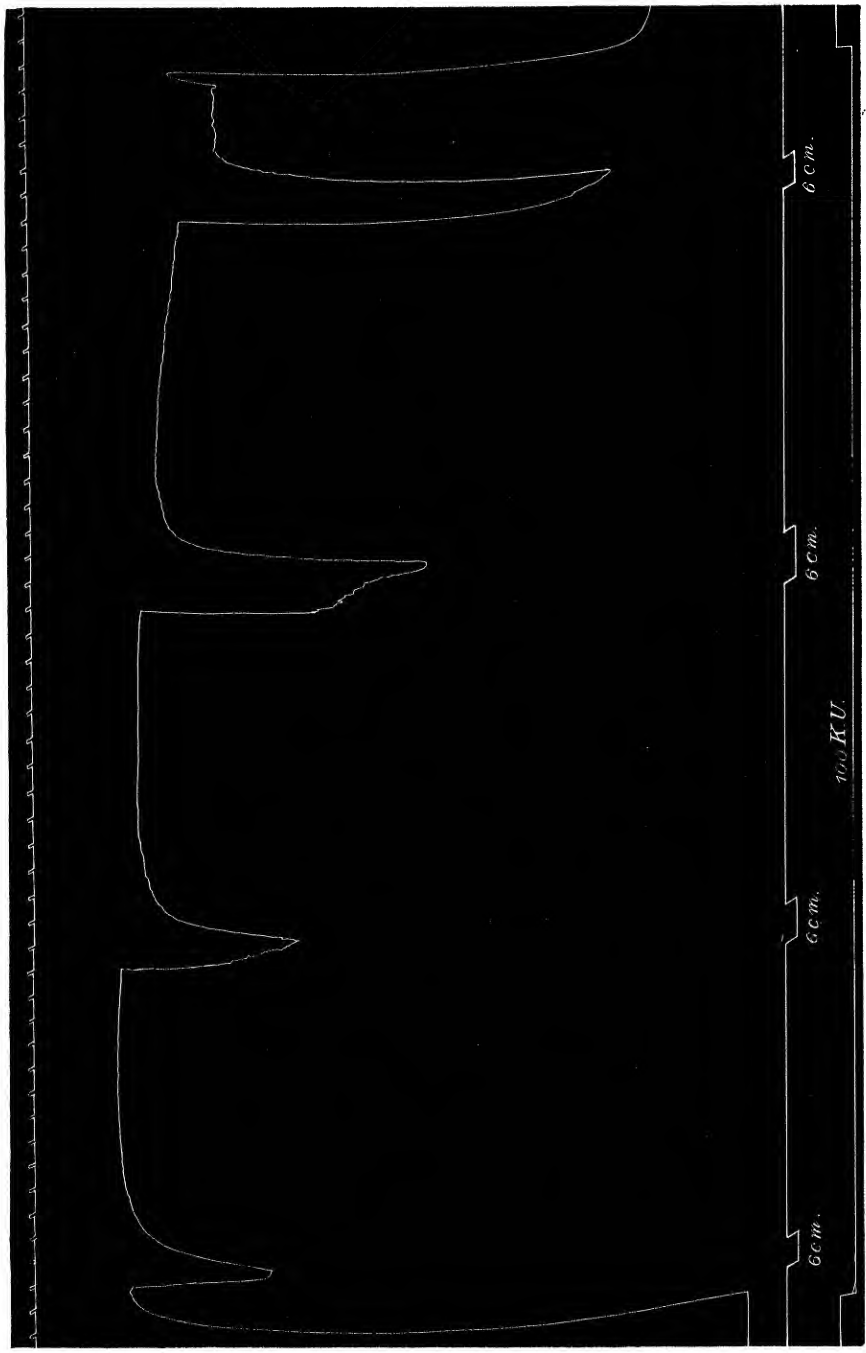

FIG. 7.—Increased inhibitory effect of a given stimulus during the progress of the background-reflex which it opposes. *Semitendinosus* (cat, decerebrate). Lower signal marks stimulation (faradic) of the ipsilateral afferent (combined peroneal-popliteal). Upper signal marks stimulation (faradic) of the contralateral afferent (combined peroneal-popliteal), this stimulus being of same intensity at all its applications, namely secondary coil at 6 cm. Time marked above, in seconds.

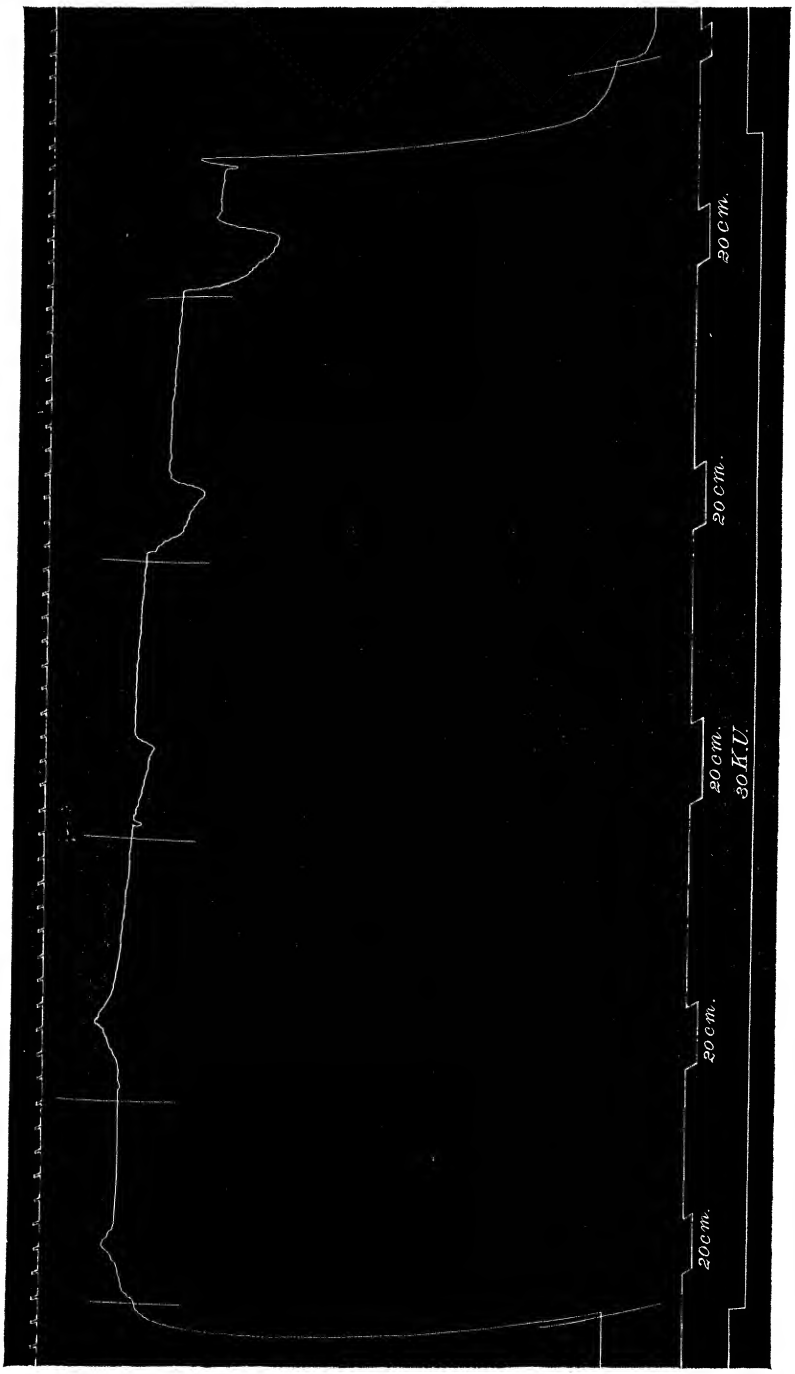

FIG. 8.—Reversal of reflex effect of a given stimulus with progress of the background-reflex. *Semitendinosus* (cat, decerebrate). Lower signal marks stimulation (faradic) of the ipsilateral afferent (combined peroneal-popliteal), intensity of stimulus being 30 Kronecker units. Upper signal marks stimulation of contralateral afferent (combined peroneal-popliteal), this stimulus being of the same intensity at all applications, namely secondary coil at 20 cm. Time marked above, in seconds.

which it often does, repetition of that same stimulus in the later course of the background contraction will produce inhibitory decrement of the background instead of excitatory increment (fig. 8, also fig. 6). In this case fatigue of the background ipsilateral stimulation actually reverses the reflex effect exerted by the contralateral afferent.

iii. *Rebound.*

With the flexor muscle and centre, as with the extensor, the withdrawal of an inhibitory stimulus is frequently followed by a motor discharge from the centre and in result a contraction of the muscle. In our

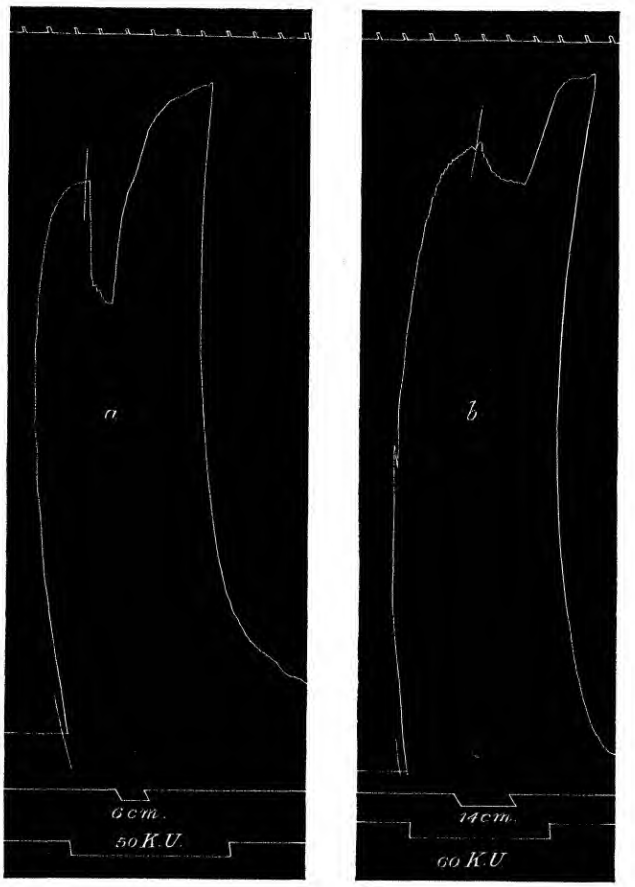

FIG. 9.—Rebound contraction. *Semitendinosus* (cat, decerebrate). Lower signal marks stimulation of ipsilateral afferent (combined peroneal-popliteal); upper signal marks stimulation of contralateral afferent (combined peroneal-popliteal). On withdrawal of the intercurrent inhibitory stimulus the reflex contraction caused by the ipsilateral stimulus increases to beyond the grade it had prior to the inhibition. Time marked above, in seconds.

observations, where the inhibitory stimulus is employed intercurrently against a background of contraction, this rebound manifests itself as increase of the background contraction to a height above that which it had prior to its depression by the intercurrent inhibition (fig. 9, also fig. 1, *c*, and fig. 6).

Circumstances favouring the exhibition of the flexor rebound are, just as in the case of extensor rebound, (1) considerable intensity of the intercurrent stimulus, (2) a somewhat brief duration of the intercurrent stimulus, (3) considerable intensity of the background stimulation.

Flexor rebound occurs not only when the background contraction is provided by electrical stimulation, but also when a "natural" reflex is in progress (fig. 6). Thus it follows intercurrent inhibition of a reflex contraction evoked by pinching the pinna of the ear, or when the reflex interrupted by the inhibition is of some source not clearly traceable in the experiment and arises apparently "spontaneously."

Marked rebound may ensue although the amount of elongation caused by the inhibitory stimulus may have been very small (fig. 10, *b*), owing to the length of the muscle at the time when the inhibitory reflex was evoked being already great. The flexor rebound in our experience does not present the prolonged tonic character which extensor rebound so often exhibits in the decerebrate preparation. The rebound contraction is short-lasting; when at all prolonged it frequently has a somewhat rhythmic form (fig. 10, *b*). In a series of somewhat quickly repeated elicitations it, like extensor rebound and even more markedly than that, diminishes rapidly. In other words, when provoked a number of times in rather rapid succession it soon tires out (fig. 6).

A point of interest in regard to the rebound is the following: As shown above, the contralateral nerve, although its predominant reflex effect on the flexor is inhibitory, does, under certain circumstances, produce instead of inhibition a weak contraction of the muscle. When this latter is its result, on withdrawal of the stimulus which has excited the weak contraction there not infrequently ensues increase of the contraction to beyond that already excited (fig. 10, *a*). In other words, rebound seems to ensue although the stimulus has excited no apparent precurrent inhibition. Possibly in these cases an inhibitory effect is really produced during the stimulus, but remains masked by concurrent excitation due to pressor fibres mixed with the inhibitory in the afferent nerve. On that supposition the rebound might still be post-inhibitory, although the inhibition was not apparent in the total result on the muscle.

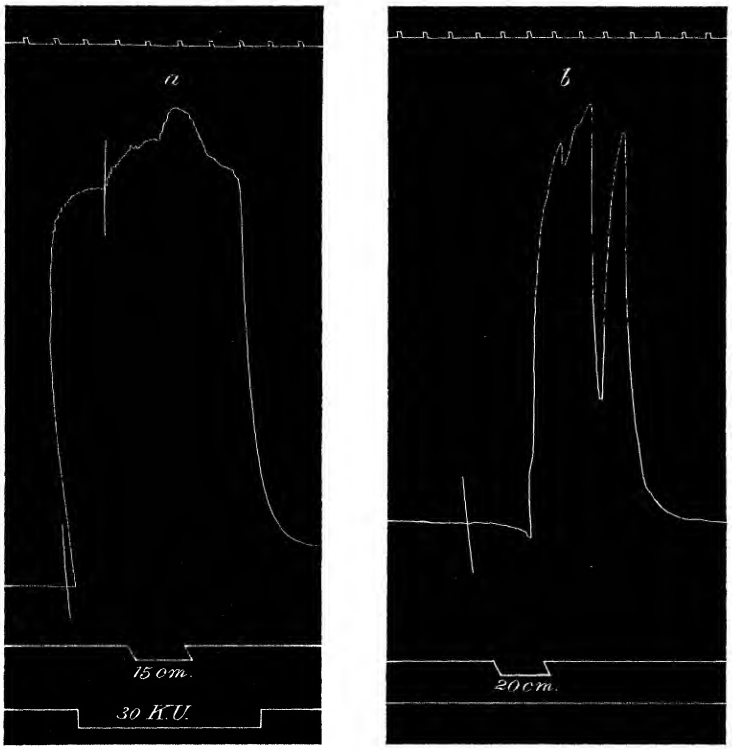

FIG. 10, *a*.—*Semitendinosus* (cat, decerebrate). Increase of intensity of the reflex background on withdrawal of a weak intercurrent stimulus whose only obvious effect had been pressor, not depressor. Lower signal marks stimulation of ipsilateral afferent; upper signal marks stimulation of contralateral afferent. Time marked above, in seconds.

FIG. 10, *b*.—Rebound after inhibitory stimulus which had, however, owing to toneless state of muscle, produced no relaxation of the muscle. *Semitendinosus* (cat, decerebrate). Upper signal shows stimulation (faradic) of contralateral afferent (combined peroneal-popliteal). The muscle at the time of application of this stimulus was resting and without apparent tonus. No obvious effect beyond questionable slight relaxations was caused by the stimulus during its application, but on its withdrawal there ensued immediately an ample though short-lasting rebound contraction. Time marked above, in seconds.

4. CONCLUSION.

Our observations show that the reflex influence of contralateral afferents (hind-limb) on the knee flexor resembles that of the ipsilateral afferents on the knee extensor.* In both cases moderate and strong stimulation produces reflex inhibition, while weak stimulation under certain conditions produces reflex contraction; and with stimuli of intensity belonging to a somewhat restricted range between weak and moderate the reflex effect is contraction

* Sherrington and Sowton, 'Roy. Soc. Proc.,' B, 1911, vol. 83, p. 435.

followed by inhibitory relaxation. In these respects, therefore, both these sets of afferents conform with that type of afferent whose reflex reactions, as Fr. Fröhlich* has pointed out in the frog, are analogous to the reactions given by the nerve of the opening muscle of the arthropod claw. A paradigm of the results may be drawn up thus:—

Afferent limb-nerve.	Muscle.	Intensity of stimulation.			
		Weak.	Intermediate.	Moderate.	Strong.
Ipsilateral	Extensor	+*	+ −	−	−
„	Flexor†		+	+	+
Contralateral	„	+*	+ −	−	−
„	Extensor‡		+	+	+

\+ signifies reflex contraction.
− signifies reflex relaxation.
\+ − signifies reflex contraction followed during the stimulation by reflex relaxation.

* Under the circumstances mentioned previously in the text.
† Sherrington, 'Journ. Physiol.,' 1910, vol. 40, p. 28.
‡ *Ibid.*

As briefly summarised in the above table it might appear that the sole factor determining whether, in these cases, reflex contraction or reflex inhibition ensued is the intensity of the stimulation. It was shown, however, in the more detailed descriptions supplied earlier in this and the previous paper† that that is really not the case. Another important determining factor appears to be the degree of the intensity of the reflex background at the time when the intercurrent reflex is tested.

* F. Fröhlich, Verworn's 'Zeitschr. f. Allgem. Physiol.,' 1909, vol. 9, p. 55.
† Sherrington and Sowton, *loc. cit.*